ON THE RELATIVE ABUNDANCE OF MIGRANTS FROM THE NORTH TEMPERATE ZONE IN TROPICAL HABITATS

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Each year beginning in July or August and continuing as late as May in the following year many areas in Latin America, Africa, and the Indomalaysian region are inundated by migrants from the nearctic or palearctic regions. Although no systematic comparative studies have been done on these areas, many comments have appeared in the literature which hint at assessment of the impact of these migrants on the tropical faunas that they visit. Unfortunately these studies vary in intensity and objectives to the extent that synthesis of results is difficult.

Willis (1966) presents an intensive study of the roles of migrants at army ant swarms, while Leck (1972a,b) discusses the impact of North American migrants at fruiting trees in Panama. Other studies in the neotropics have been concerned with ecological isolation in wintering warblers (Lack and Lack 1972), or the impact of migrants on seasonal breeding cycles (Miller 1963). Tramer (1974) presented data on proportions of wintering North American birds in dry habitats in tropical Mexico. Many studies in Africa have dealt with the seasonal movement patterns, distributions, and/or abundance of palearctic migrants (Morel and Bourliere 1962, Elgood et al. 1966, Brosset 1968, Morel 1968, Pearson 1971, Britton 1974, Thiollay 1970a,b). Moreau (1972) presents an excellent summary of what is known of the Palearctic-African bird migration system. In Asia little is known of the impact of migrant birds on their host ecosystems. Ward (1968, 1969) comments briefly on the significance of the influx of migrants on the annual cycle of Malaysian birds, as does Brosset (1968) on the abundance of migrants in India. The extensive studies of McClure and Medway have contributed materially to the clarification of migration of Palearctic species to Southeast Asia (McClure 1964, 1974, McClure and bin Othman 1965, Medway 1972, Nisbet and Medway 1972).

Unfortunately, few of these studies adequately define the habitats under consideration, the size of area examined, *and* the densities of tropical resident and migrant species in the same area. Although these individual studies are often excellent, it is difficult to derive a comparative synthesis from their results.

Between 1968 and 1972 I visited a number of forest areas on several continents as part of a study of the organization of tropical forest avifaunas. A routine procedure in each area involved use of mist-nets at 0–2 m. In this

paper I present results which relate to the impact of northern migrants in the tropics. Initially, I present data from a number of habitats studied intensively in Panama. Subsequently, more restricted data from Africa and Indomalaysia are presented. Finally, I attempt a summary of the scattered literature on north temperate migrants in the tropics.

"Tropical resident" refers to species that reside throughout the year in the region of the study area. Although it is not widely recognized, many of these species show considerable propensity for seasonal movements (Moreau 1972, Elgood et al. 1966, Karr 1976a). "Migrants" will refer to species that move long distances and chiefly to species that breed in the north temperate zone and spend the temperate winter in the tropics. These species may occur as "transients" on an area or as "winter visitors." "Winter visitors" occur as residents in a study area for some period of time, especially in the December to February period. Generally, the status "winter visitor" is used when reasonable evidence of winter residence is available, e.g. when a banded bird is captured on several occasions or a bird is observed through a regular molt sequence.

There is a tendency for biologists with a primarily temperate zone background to refer to these migrants as temperate-zone birds when what is meant is temperate-zone breeders. Clearly, this phraseology should be so understood since these birds spend nearly as much time, and in some cases more time, on their tropical wintering grounds as they do on the north temperate breeding grounds. I will focus on the birds of terrestrial environments and not consider migrant shorebirds, although shorebirds will be included in discussions of Panama study areas so that data are complete.

FIELD METHODS

Panama study areas.—The data presented in this paper derive from a combination of field techniques (Karr 1971a). Study plots in Panama were surveyed from July 1968 through July 1969 by walking the study areas for several hours, usually in the morning, and recording on maps the location and species of all birds. Mist-nets were used in shrub and forest habitats to clarify ambiguities about species composition and abundance. Generally, twelve 30 and/or 36 mm mesh nets, 12 m long were placed in the study area with the lower shelf on the ground.

Nets were opened 30 to 90 min before sunrise and checked hourly until about noon when they were closed for the day. Birds captured in the nets were identified, weighed, individually marked, and released at the capture site. Generally, a color slide was taken of each species captured to confirm identifications.

Since migrant birds do not sing regularly during this period and many are only transient on the intensive study areas, no attempts were made to quantify abundance of the migrant species from census data. A reasonable index of their abundance relative to the resident birds can be obtained if we assume that both migrants and residents are captured in mist-nets in proportion to their abundance. Migrants may be captured with somewhat higher frequency than expected by their abundance since they may be moving

more than residents (see below). The ratio of migrant individuals to total individuals captured should be a reasonable first approximation of migrant densities.

African and Asian study areas.—Most of the study areas in Africa and Asia were mist-netted for relatively short periods so comprehensive censuses were generally not possible. However, I used mist-nets as described above for several days on each study area.

STUDY AREAS

Extensive discussions of the study areas have been presented previously for the Panamanian (Karr 1971a) and African (Karr 1975, 1976b) study areas. All Panama study areas were in the lowlands. Vegetation types varied from grassland to forest. There were 2 grazed and 2 ungrazed grassland study areas. Two shrub areas included mosaics of grass and thicket habitat; early shrub was predominated by grass, while a late shrub area was a similar mosaic with shrubs predominating. Temperatures near all of the study areas averaged near 27°C, but rainfall was somewhat higher in the forest (2600 mm) than near the grasslands (1900 mm) or shrub areas (2000 mm).

In Liberia I studied birds of several study areas near Mt. Nimba at 500 m. The study areas included forest and late shrub similar in vegetation structure to the Panamanian sites, and an intermediate area of disturbed forest. Mean annual temperature in the vicinity of each study area is near 23°C with annual rainfall slightly below 3000 mm. The only other African site visited during the season when Palearctic migrants might be expected was the Sokoke Forest in coastal Kenya about 90 km north of Mombasa. This is a coastal deciduous forest growing on a dry sandy soil.

I netted in only one forest in India. This area, located near the athletic field at Mahabaleshwar in Maharashtra (17° 56′ N, 73° 40′ E), is part of the western Ghat forest that extends from just south of Bombay to the southern tip of India. At 1370 m the forest has a distinctly montane appearance with a canopy height of about 15 m. The sparse ground cover of the area is similar to that of lowland forest. Signs of recent human (wood-gathering) and cattle activity were common. Vegetation cover was low in the 1–5 m levels and canopy coverage reached a maximum of about 60% at 6–15 m. Mahabaleshwar has a mean annual temperature of about 19.5°C and an annual rainfall of 6200 mm, with most of the rain falling in the June to September monsoon period. Common trees in the forest around Mahabaleshwar include *Syzigium cumini, Memecylon edule, Actinodaphne hookeri, Randia brandisi, Lassiosiphon ericephalus, Glochidia hohenackeri,* and *Mappia foetida.*

I also netted in the Pasoh Forest Reserve, about 72 km from Kuala Lumpur, Malaysia. This relatively undisturbed reserve is used in an intensive study of the dynamics and productivity of lowland dipterocarp rain forest as part of a Malaysian/United Kingdom contribution to the International Biological Program. The study area is located at about 2° 59′ N, 102° 18′ E at an elevation of less than 100 m. The mean annual temperature at nearby Kuala Pilah is near 26°C and annual rainfall averages near 1900 mm. Trees on the area include many species with *Shorea* spp. and *Dipterocarpus* spp. being especially abundant. Canopy height commonly exceeds 40 m.

RESULTS

Seasonal distribution of migrants to Panama.—Before the end of the North American summer the first migrants begin to arrive in central Panama. Upland Sandpiper (*Bartramia longicauda*) and one of the northern forms of the
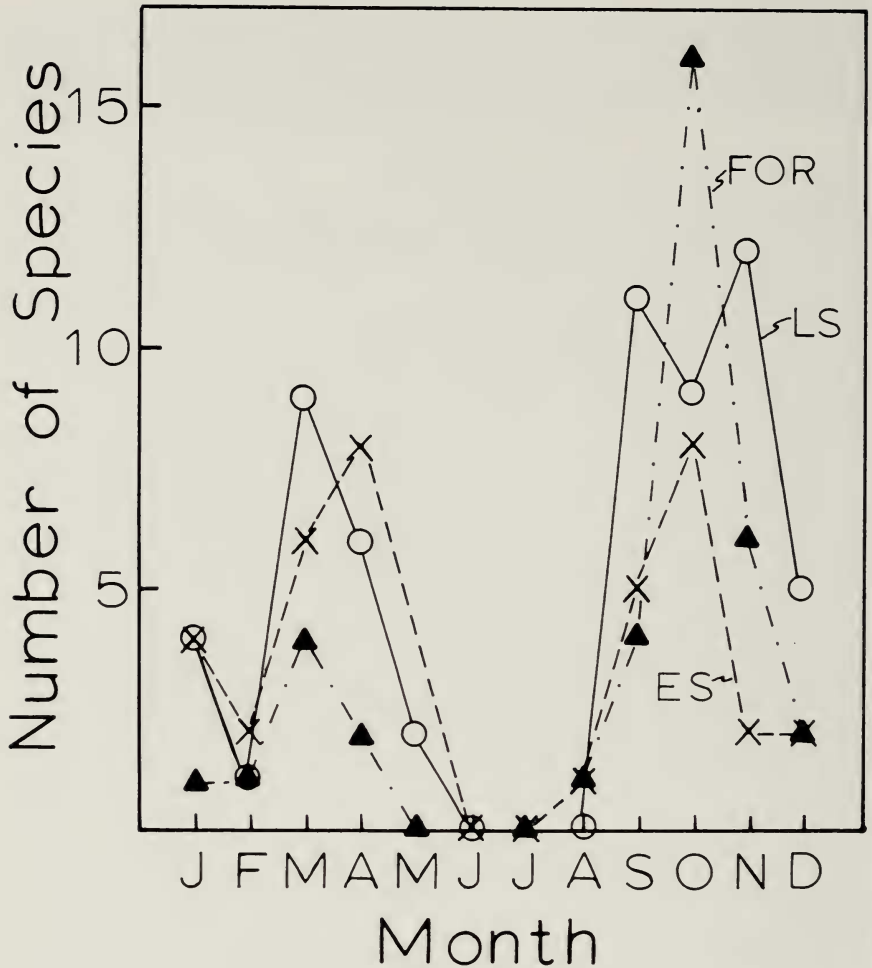
FIG. 1. Number of migrant species seen in each month on the early shrub (ES), late shrub (LS), and forest (FOR) study areas in central Panama.

Rough-winged Swallow (*Stelgidopteryx ruficollis*) are first seen in the grasslands in August. September through November are peak months with several species of sandpipers, flycatchers, and warblers as well as the Barn Swallow (*Hirundo rustica*) arriving in September. There is a sharp decline in the number of migrant species from December to February (Fig. 1).

The influx of northward moving species begins in late February or early March and peaks in April. In the forest the movement apparently has stopped

before May but 2 species from northern Middle America are still noted in the shrub areas well into May (Table 1, Fig. 1). No north temperate breeding species were seen in the study areas in June or July. The fall peak in number of migrant species was about 30% higher than the spring peak in the 2 shrub habitats and 400% higher in the forest. The spring peak was more protracted than the fall peak. However, many species that were abundant in the fall, especially thrushes and warblers, were rare or not observed on my study areas in the spring.

Migrant species on the Panama study areas.—Species that visited the Panama study areas either as non-breeding transients or as winter visitors are classed as migrants. Most of these species breed north of Panama, either in temperate North America or in 4 cases in northern Middle America or the West Indies. One species, the swallow *Phaeoprogne tapera*, is a visitor from southern South America during the southern hemisphere winter. The number of migrant species varied from as few as 5 on the dry grazed grassland to a high of 28 on the late shrub area (Table 1). Those on the dry grazed grassland were mostly swallows (4 spp.) but included the Yellow-rumped Warbler (*Dendroica coronata*). This warbler, a very irregular, sporadic winter visitant to Panama, was observed in late December and January. Migrants on the wetter portion of the grazed study areas included 4 sandpipers, 1 snipe, 4 swallows, an icterid (*Dolichonyx*) and the Yellow-rumped Warbler. The ungrazed study areas had similar groups of species but added 1 raptor, and 2 tyrant-flycatchers.

The early shrub migrants included 6 Falconiformes, 6 tyrant-flycatchers, 3 swallows, 6 wood-warblers, and 1 each of thrush, vireo, and tanager (Table 1). The late shrub study area had a similar species distribution with 10 wood-warblers. Twenty-three of 25 migrants observed on the early shrub area and 25 of 28 on the late shrub were from North America. One migrant from South America (*Phaeoprogne*) occurred on both areas. One on the early shrub and 2 on the late shrub were from northern Central America.

I observed 22 migrant species on the forest study area (Table 1). The species were similar to those on the shrub areas, but included more thrushes.

I observed 48 migrant species (seen, heard, or netted) on all study plots, although most occurred as transients, rather than as winter visitors.

Relative abundance of migrants and residents.—Total winter densities of migrant species are difficult to assess because of the mobility of many species and problems of visibility. However, mist-nets operated in the undergrowth of shrub and forest habitats can provide an index of migrant abundances.

On the Pipeline Road forest study area, no migrants were captured in September but nearly one-fourth of the individuals captured in October were migrants (Table 2). The capture rate declined for 2 months, increased

TABLE 1

MIGRANT SPECIES RECORDED ON THE STUDY AREAS IN CENTRAL PANAMA.†

| Species | Grassland | | | | Early Shrub | Late Shrub | Moist Forest |
| | Grazed | | Ungrazed | | | | |
	Dry	Wet	Dry	Wet			
Ictinia misisippiensis					4		
I. plumbea**						3,4,5	8,9
Buteo swainsonii					3	3	9,10,11
B. platypterus					4,5	3,4,11	9,10,11
Circus cyaneus			3,11				
Falco peregrinus					3	3	
F. sparverius					10		
Charadrius wilsonia			4,5				
Bartramia longicauda		4	4,8,9,10	4			
Tringa melanoleuca		9					
T. solitaria		9					
Actitis macularia		9					
Capella gallinago	11						
Calidris melanotos			10				
Muscivora tyrannus**		9			9	9	

TABLE 1. (*Continued*)

Species	Grassland				Early Shrub	Late Shrub	Moist Forest
	Grazed		Ungrazed				
	Dry	Wet	Dry	Wet			
Tyrannus tyrannus			4	4	3,4,5	4,5,9	9,10
*T. dominicensis***			3	3			
*Myiodynastes luteiventris***						9	
Myiarchus crinitus					1,10	1,3,11,12	10
Contopus virens					8,9,10,11	9,10,11	10
Empidonax virescens					1,4,10	4,9,11	11
E. traillii					1,4,10	4,9	
Petrochelidon pyrrhonota	3,5	3,5	10	10			
Hirundo rustica	3,5,10,11,12	3,5,10,11,12	4,10,11	4,10,11	3,4,5,9,10	9,10	
Stelgidopteryx ruficollis	3	3	8	8	3,4	3,4	
Riparia riparia	4	4	5,10	5,10			
*Phaeoprogne tapera**					2	2	
Catharus ustulata						10,11	3,4,10,11
C. minima					10		10
C. fuscescens							10,11
Vireo olivaceus					9	10	10

TABLE 1. (Continued)

| Species | Grassland | | | | Early Shrub | Late Shrub | Moist Forest |
| | Grazed | | Ungrazed | | | | |
	Dry	Wet	Dry	Wet			
V. flavifrons						12	
Mniotilta varia					11	10,11,12	10
Vermivora peregrina					12	1,11,12	10,12
Dendroica pensylvanica					1,12	10,11,12	1,3
D. coronata	1,12	1					
D. castanea						10	10
D. petechia					9	1,3,9,10,12	
Seiurus aurocapillus					10		
S. noveboracensis						9,11	4
Oporornis formosus						9,11	2,3,4,10,11,12
O. philadelphia						3	
Wilsonia canadensis					10	10,11	10
Setophaga ruticilla						9	11
Icterus galbula							10
Piranga rubra					2	1,3,11	10
Dolichonyx orizyiorus		11		10			
Pheucticus ludovicianus							3
Total Number of Migrants	5	11	10	8	24	28	22

† Coded by month from January (1) through December (12).
* Migrant from southern South America.
** Migrant from northern Middle America.
*** Migrant from South Florida or West Indies.

TABLE 2

DISTRIBUTION OF INDIVIDUALS AND SPECIES AMONG RESIDENT AND MIGRANT SPECIES IN PANAMA MIST-NET STUDIES

Study Area (Habitat)	Month	# Net Hours	Total Number Captures	Number of Captures		Number of Species		Captures/Species		% Migrant Individuals	Captures/Hour	
				R[1]	M	R	M	R	M		R	M
Pipeline Road (Lowland Forest)	Sept.	126	61	61	0	26	0	2.3	0.0	0.0	.48	.00
	Oct.	258	120	93	27	31	5	3.0	5.4	22.5	.36	.10
	Nov.	238	91	85	6	31	3	2.7	2.0	6.6	.36	.03
	Dec.	201	84	82	2	28	1	2.9	2.0	2.4	.41	.01
	Feb.	149	44	41	3	24	1	1.7	3.0	6.8	.28	.02
	Mar.	280	72	70	2	28	2	2.5	1.0	2.8	.25	.01
	Apr.	129	53	52	1	22	1	2.4	1.0	1.9	.40	.01
	May	192	73	73	0	22	0	3.3	0.0	0.0	.38	.00
Chiva Chiva Road (Late Shrub)	Sept.	92	46	42	4	18	3	2.3	1.3	8.7	.46	.04
	Oct.	139	82	73	9	32	7	2.3	1.3	11.0	.53	.06
	Nov.	102	45	43	2	23	2	1.9	1.0	4.0	.42	.02
Fort Clayton (Disturbed Forest)	Oct.	108	59	29	30	18	8	1.6	3.8	50.8	.27	.28
End of Chiva Chiva Road (Disturbed Forest)	Dec.	165	115	107	8	36	4	3.0	2.0	7.0	.65	.05
Puercos Island (Island Forest)	Jan.	547	110	83	27	14	5	5.9	5.4	24.5	.15	.05

[1] R = resident, M = migrant.

slightly in February, and again declined. Seven of the 14 captures from November to April were of a single Kentucky Warbler (*Oporornis formosus*) (Karr 1971b).

Mist-net data for the late shrub study area are limited to the late rainy season (September to November) (Table 2). Netting activities on the shrub area were restricted to this season because of the danger of losing nets and birds to fires during the dry season (December–April). October capture rates were highest in this area but less than for the same month in the forest.

Mist-net data for 2 other mainland areas are available for comparison (Table 2). Both areas had disturbed forest with denser undergrowth than that on the Pipeline Road study area. The first area, located on Fort Clayton, was netted in October of 1968. Fifty-nine birds were captured in 2 mornings (8 migrant species, 30 individuals; 18 resident species, 29 individuals).

A similar area on Chiva Chiva Road was netted in December. Only 8 of 115 captures (7%) were of migrants. These 8 captures included 4 species: *Oporornis formosus, Seiurus noveboracensis, Empidonax traillii,* and *Helmitheros vermivora.* I captured 36 resident species.

The migration peak occurred in October in all habitats, and involved the largest number of species and individuals in forest habitats. At mist-net levels (0–2 m) migrants made up about 20% of the avifauna, but were as high as 50% in some areas (Ft. Clayton).

September data indicate that early migrants seemed to favor the shrub habitat (9% of captures) rather than forest (no captures). The fact that net captures in the shrub area began almost a week before that in the forest strengthens that conclusion. Later in the migration season relative densities of migrants in shrub habitat exceeded those in forest areas.

An index of the relative rarity of the migrants can be obtained by determining captures per species for migrant and resident species (Table 2). It is clear that the migrant species are generally rarer than their resident counterparts, despite the general rarity of tropical forest species (Karr 1971a). Major exceptions to this pattern occurred in the peak migration months of October and February when the number of individuals per species was higher for migrants than for residents.

Summarizing data from the Panama studies, migrants reached their greatest proportion of the community in forest during the peak of the fall migration. However they wintered at higher densities in areas which contained a mixture of second growth and disturbed forest than in extensive areas of mature forest. A few species occurred as transients in (or over) grassland habitats, but none were winter visitors on grassland study plots.

Migrants on the African study areas.—Three study areas netted in Liberia —lowland forest (relatively undisturbed), disturbed forest, and late shrub—

were chosen to correspond to the areas studied in Panama (Table 3). Samples on these areas included from 295 to 650 mist-net hours; not a single capture of a Palearctic migrant was made (Table 3). This includes both forest and late shrub habitats. (The late shrub area had been relatively undisturbed for 6 years.) Nearby grassland and garden areas however contained many migrant species (25+) and individuals during my visit.

Similarly, in East Africa many migrants were observed in savanna and grassland habitats but a mist-net sample in the coastal deciduous forest of Kenya yielded no migrants (Table 3).

During 7 months of field work in Africa when migrants were present, I did not observe a Palearctic migrant in wet forest habitat. On one occasion I observed the cuckoo *Clamator levaillantii* about 15 m inside a forest in Liberia. This is unusual, however, as this migrant from within the Ethiopian region (breeds in the drier areas of Africa south of the Sahara) is more commonly found in open habitat.

Migrants on Indomalaysian study areas.—Mist-netting at Mahabaleshwar, India during January of 1972 yielded capture rates of about one bird per 10 mist-net-hours (Table 3). Forests in Liberia and Panama yielded one bird per 2–4 hours. Clearly the total populations of the Indian forest are significantly below those for lowland forests on the other 2 continents. My limited experience at netting in mid-elevation forests (1000 m) in the neotropics yielded very high capture rates. In 3 days of netting at San Vito in southern Costa Rica, I captured one bird every 1.5 hr. (Unfortunately these Costa Rican data were collected in the north temperate summer—July—so no migrants were present.) A brief netting attempt in forest at Wau, New Guinea in May gave capture rates similar to those of the San Vito site. No migrants were included in the New Guinea sample, but palearctic migrants and migrants from Australia are relatively rare in New Guinea except for some aquatic forms and 2 swifts (Rand and Gilliard 1967). Generally New Guinea resembles Africa in the absence of migrants from rainforest although migrants are often abundant in open habitats at low and medium elevations and on some satellite islands (Diamond 1975; pers. comm.).

The low densities of birds in the Indian forest are particularly striking when one considers that 10 of 18 birds captured were migrants. Although I did not net in other Indian forests, surveys of forest areas near Bombay, Baroda, New Delhi, Agra, Varanasi, and Calcutta had low resident abundance and high abundance of Palearctic migrants. Generally these were relatively open, dry forests. In south India at Manjolai in Tamil Nadu, residents appeared higher and migrants lower in abundance than in northern India, but I have no quantitative data for this region.

In March 1972 I visited 2 areas in Malaysia. In 3 days of netting at the

TABLE 3

DISTRIBUTION OF INDIVIDUALS AND SPECIES AMONG RESIDENT AND MIGRANT SPECIES IN AFRICAN AND INDOMALAYSIAN MIST-NET STUDIES

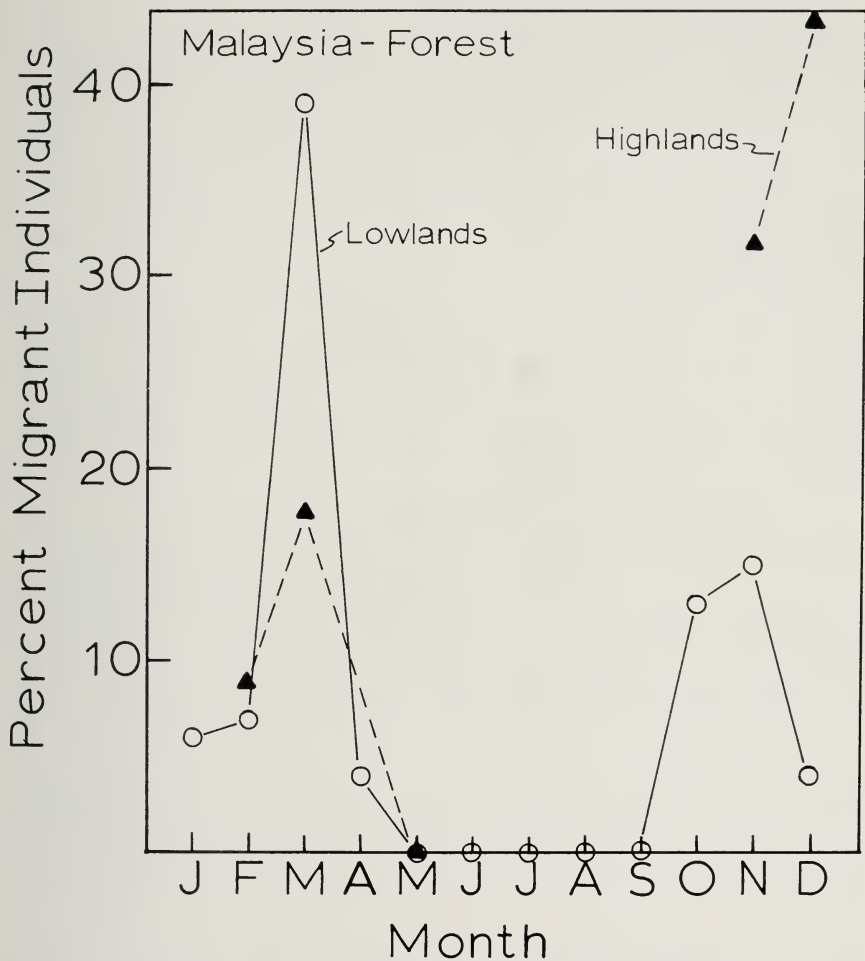| Country	Study Area (Habitat)	Month	Number of Net Hours	Total Number Captures	Number of Captures		Number of Species		Captures/ Species		% Migrant Individuals	Captures/Hour	
					R[1]	M	R	M	R	M		R	M
Liberia	Airport Forest (Lowland Forest)	Feb. thru Apr.	650	194	194	0	38	0	5.1	0.0	0.0	.30	0
	Forest Road I (Disturbed Forest)	Apr.	295	84	84	0	23	0	3.7	0.0	0.0	.28	0
	Forest Road II (Late Shrub)	Mar. thru Apr.	374	131	131	0	30	0	4.4	0.0	0.0	.35	0
Kenya	Sokoke (Coastal Semideciduous Forest)	Nov.	176	33	33	0	11	0	3.0	0.0	0.0	.19	0
India	Mahabaleshwar (Lower Montane Forest)	Jan.	179	18	8	10	4	3	2.0	3.3	55.5	.04	.06
Malaysia	Pasoh (Lowland Forest)	Feb. Mar.	≈1500 211	185 36	152 33	33 3	34 14	4 2	4.5 2.4	8.3 1.5	17.8 8.3	.11 .16	.02 .01

[1] R = resident; M = migrant.

Fig. 2. Percent migrant individuals in mist-net samples from the lowlands and high-
lands of Malaysia. (From data in McClure 1964 and McClure and bin Othman 1965.)

Pasoh forest I captured 36 birds in 211 hours (1 bird per 6 hours) (Table 3).
Only 3 of the individuals (8.3%) were migrants. Dr. David Wells of the
University of Malaya kindly provided me with an extensive set of data for
a mist-net sample from the same forest area. His data, collected in February,
include 33 migrants in 185 captures (17.8% migrants; Table 3). Although
the exact number of net hours is not known, about 1500 hours of netting
were conducted during the daylight hours of 4 days, yielding a capture rate
of about one bird every 8 net hours.

I have limited mist-net data for another Malaysian forest site—Bukit Lanjang—which has been studied by the Institute for Medical Research at Kuala Lumpur. I netted in this area in mid-March and caught 40 birds in 3 days (160 net hours), giving the highest capture rate of the Asian samples at 1 bird per 4 net hours. Intensive research in this area for several years has resulted in a modified foliage configuration. From experience in the neotropics in similar circumstances I expected capture rates higher than at Pasoh. Although I expected high migrant densities, no migrants were among the 40 captures.

In summary, these observations from the Indomalaysian region suggest 2 major points: (1) for those species sampled by ground level mist-nets, densities of birds in Indomalaysian forests are significantly below those in African and neotropical forests; and (2) winter densities of migrants are higher in lowland and mid-elevation Indomalaysian forests than in similar African and neotropical habitats.

<div style="text-align:center">DISCUSSION</div>

This and other studies clearly indicate several general patterns with respect to the magnitude of interactions between migrant and resident birds in tropical environments. There are (1) seasonal changes in number of migrants in the tropics that are correlated with changes in available food supply on their temperate breeding ground. In addition, the importance of migrants varies with (2) vegetation type, (3) elevation, and (4) food type within each of the major geographical areas. Finally, there is variation (5) among the continents and (6) between continents and adjacent islands in the significance and abundance of migrants. Other factors which may influence patterns of migration such as climate, distance, shape and position of host continent, topography, and location and orientation of mountain masses will not be discussed here. In the following discussion I shall summarize my own observations and will also freely draw on the studies of many others. No doubt many significant studies have been overlooked in this review, and much unpublished, relevant work is not cited. The volume of relevant literature is tremendous, and scattered in many publications. My apologies to those whose work I have overlooked.

Seasonal abundance of migrants.—Very few migrants occur in tropical areas from May to August. (For this and subsequent discussion, I exclude the shorebirds, osprey, and larids. Some individuals of these species spend the north temperate summer in Panama.) A few early arrivals are often noted in August and some of the last individuals to depart may remain into early May. October is generally the month of greatest migrant density as transients predominate (this study, Galindo and Mendez 1965, Morel 1968,

Willis 1966, Leck 1972a). After the October peak, wintering densities are generally low. An increase occurs in the northward spring migration that is well below the fall peak in both number of species and number of individuals (Table 2, Fig. 1). In perhaps the most intensive study to date, Willis (pers. comm.) found that about 12% of the individuals on Barro Colorado Island were migrants in October. However, only 4% of the biomass was migrants as the average migrant individual is smaller than the average resident individual. One difficulty in interpreting the seasonal results of Willis is that they are for a composite of forest, second growth, and aquatic habitats. The low numbers of northward moving birds in March through May result from most species returning by the more direct route over the West Indies (Smith 1975). In addition, some migrants to Panama change habitats during the north temperate winter as food availabilities change (E. Morton, pers. comm.).

Peak migrant abundances in African savanna occurred in October with 47 individuals per 25 ha (Morel 1968). Rather than a decline followed by an increase in the spring migration as observed in Panama, there was a general decline until the next spring when all individuals had departed. This decline was presumably due to the long dry season in Morel's area which begins in late September and continues for 8–9 months.

In gallery forest migrant abundances were high in October, decreased in the November to January period, and then increased in the north temperate spring (Morel 1968). Morel attributed this to the movement of birds from the nearby savanna into the gallery forest where food resources were more abundant and regularly available.

In western Kenya the abundance of migrants in secondary thicket habitat declined from 60% of individuals (50% of biomass) in the fall passage period to 27% of individuals and 25% of biomass in the winter (Britton 1974). Similar seasonal changes occurred in acacia and cultivated habitats studied by Britton.

In the lowlands of southeast Asia the peak in migrant abundance occurred in March (39% of captures) (Fig. 2). Another peak occurs in November but it appears to be somewhat smaller than the March peak (McClure and bin Othman 1965). Densities in the overwintering period (December to February) are lower, averaging about 6% of captures. Generally only 1 or 2 migrant species are represented in these samples. At 1500 m on Mt. Binchang, McClure (1964) recorded the highest migrant densities (35–40% of captures) in November and December with lower densities in February and March (5–18%).

Vegetation type.—Several workers have examined changing abundances of migrants among habitats or vegetation types. Most recently Tramer (1974) determined the abundances of migrants and residents in dry tropical habitats

in the Yucatan peninsula of Mexico. His studies were conducted on disturbed (garden), partly disturbed, and undisturbed habitats. Densities ranged from 3 to 8 birds per ha in the disturbed and undisturbed areas. Excluding one coastal study area, migrant species made up from about 8 to 36% of the individuals in his communities. The variance was high among study areas with the same degree of disturbance. In a study of wintering parulids in Jamaica, Lack and Lack (1972) tabulated the number of warblers of a variety of species seen per hour in several different vegetation types. In the wet lowlands, mangrove (12.4 warblers/10 hrs) and lowland park and garden habitats (9.0 warblers/10 hrs) yielded migrants at the most rapid rate and lowland forest (1.5) had relatively smaller numbers of parulids. A similar tabulation for limestone forest indicated the greatest abundances in periodically flooded areas at sea level (15.5). In riverine forest they observed 10.9 wintering warblers per 10 hours. Moderately moist secondary and cutover areas yielded birds at a more rapid rate (4.7–9.6) than did arid areas (0.7–2.5 birds per 10 hours). Tramer (1974) found his lowest density of migrants in a disturbed coastal area bordered by mangrove, while mangrove and flooded sea level forest had the highest migrant densities in the study by Lack and Lack (1972).

Migrants are more abundant in scrub and early forest habitats although they do use forest habitats to some extent, particularly in the northern portions of Central America (Willis 1966, pers. comm.). Moving to the south Willis found that the abundance of migrants decreased in tall forest. In South American forest, migrants were very rare, and in the Amazonian lowlands even forest edges and second growth had few migrants (Willis 1966). As discussed below this may be due to the cost of continued migration exceeding the disadvantage of staying in Middle America.

On Barro Colorado Island residents exceed migrant densities (including transients) in virtually all habitats. In old forest there are 26 resident individuals for each migrant while the numbers decrease to 12 to 1 and 2 to 1 for young forest and scrub habitats, respectively (Willis, pers. comm.).

I did not find any species of migrant that regularly used grassland habitats for wintering in my Central American studies but it was common to see large numbers of migrants in the dense thickets associated with riverine habitats. Similarly, Willis (pers. comm.) found that migrants were about 8% of the individuals in lakeshore habitats. In another paper (Karr 1976b), I have suggested that these riverine habitats may have played a significant role in the evolution of a distinct forest edge avifauna in Central America, while no such forest edge fauna seems to have developed in Africa. Perhaps riverine habitats also have been important in providing a wintering ground for migrants from North America. The activities of man in clearing of forests

(Slud 1960) during the last 10,000 to 20,000 years may have increased the habitat available to these 2 groups of birds. As E. S. Morton has emphasized (pers. comm.) large areas of cleared forest are not optimal for migrants; rather many migrants are well adapted to using mosaics of cut over and mature forest.

In Africa, also, there are significant variations in the density of migrants with vegetation type. As early as 1952, Moreau pointed out that desert and evergreen forest habitats supported few if any Palearctic migrants. In a comprehensive analysis of the Palearctic migrants of Nigeria, Elgood et al. (1966) found that most species winter in dry woodlands (Guinea savanna) and in the semi-arid (Sahel) savanna. These 2 habitats and "derived savanna" (savanna modified by human disturbance) each contained 20 or more wintering species. Coastal habitats in Nigeria (including mangrove) harbored 14 Palearctic species. Mangrove forests of the Gambia were found to contain large numbers of migrants (Cawkell 1964, Cawkell and Moreau 1963). For the terrestrial birds of the Accra Plains in Ghana, about 15% of the species are migrants, including both Palearctic and Ethiopian birds that do not breed in Ghana (Grimes 1972). In general, the results of Elgood et al. (1966) — most migrant species winter in savanna and dry woodland habitats—agree with studies throughout Africa (Morel and Bourliere 1962, Brosset 1968, Morel 1968, Pearson 1971, Thiollay 1970a,b, Moreau 1972, Karr this study and pers. obs.). Neotropical birds use cutover, parkland, and late second growth in areas of high rainfall while relatively few Palearctic migrants in Africa use the rarer high rainfall habitats. Rather they prefer the more open dry savanna and parkland areas, habitats that are little used by migrants in the neotropics.

A few studies in Africa have presented quantitative data on the densities of migrants, either absolutely or relative to resident species. Elgood et al. (1966) suggest that there may be 78 migrants per km^2 in Nigeria. Moreau (1972) uses this figure in one derivation of his estimate of 5000 million Palearctic migrants entering sub-Saharan Africa. Regrettably, this becomes circular as Elgood et al. used a 1961 estimate of Moreau's to derive their estimate of 78 per km^2. Moreau (1972) cites estimates of Pearson (1971) that wintering passerines number 2 to 5 per ha in cultivated areas. In the rank grass adjacent to the lake at Kampala, Uganda he estimated densities of 75 per ha with densities somewhat lower (about 25) in a variety of habitats near the lake. However, I found no references to densities of wintering passerines in Pearson (1971).

Several habitats studied by Britton (1974) in western Kenya contained strikingly different numbers of wintering migrants. In second-growth thickets, for example, 27% of passerines were migrants. In lowland wet forest 2%

were migrants (mostly at forest edge) while cultivated and acacia habitats had 18–19% migrants.

In West Africa the best studies are those of Morel in Senegal and Thiollay in Ivory Coast. Morel (1968) found that Palearctic migrants made up about 43% of the wintering individuals in dry acacia savanna of Senegal. Of the 97 species in his 25 ha study area, 32% (31 species) were migrants. In his gallery forest Morel (1968) found considerable year to year variation in the densities of wintering individuals. In the December to February periods of 1960 to 1962 he found densities varying from 9.5 to 20.5 per ha, which varied from 11 to 33% of the birds on the area. In a similar study of the Lamto savanna in Ivory Coast, Thiollay (1970a,b) found 165 species of birds with only 7% (11) of the species being migrants from the Palearctic. If one considers all migrants (Palearctic and Ethiopian), 30 species (18% of the fauna) are "grands migrateurs." According to Thiollay (1970a,b) densities of migrants on his savanna are much lower than those of Morel in Senegal mentioned above—only 6% of the species and 5% of the individuals. Several reasons for this striking dichotomy can be suggested. First, it is possible that the relative isolation of the Lamto savanna "protects" it from the large influx of migrants. Second, perhaps the increased distance to be travelled may limit the number of migrants that reach Lamto.

Willis (1966) suggested that the decline in migrants in Amazonia is due to the "general decline in numbers of migrants away from" North America. Since migration is so costly, it would be to each bird's advantage to end migration as soon as possible. This is especially true if mortalities on the wintering ground are as low as indicated below. If food resources are adequate in Middle America and the West Indies, little migration to South America would be expected. It seems unlikely that lack of food resources in the north prevents the movement of migrants into coastal areas of West Africa. When such West African areas contain savanna habitats many migrants are present. For example, a number of migrants visit the Accra plains of Ghana (Grimes 1972), and within a few years of the clearing of forest at Mt. Nimba in Liberia many migrants had moved into the newly opened grassland areas (Forbes-Watson, pers. comm.; Karr, pers. obs.). In addition many of the migrant species go farther south in the East African portion of their wintering grounds. For example, see maps in Moreau (1972) for *Oenanthe oenanthe* and *Saxicola rubetra*. A third and more reasonable alternative is suggested by Willis (1966); that is, migrants are not able to encroach in relatively stable areas. They are better able to "exploit environmental irregularity." From my own observations at Lamto I suspect that the complex interdigitation of ronier palm savanna and gallery forest habitats allows many species to get through the most severe season in much the same way that many

insects survive the dry season better in areas where gallery forest is available (Janzen 1973). This seems to be true in Senegal (Morel 1968).

Relatively few studies seem to have been done on the numbers of species of migrants and their abundances in the Indomalaysian region. Brosset (1968) indicates that migrants are particularly numerous in Indian habitats, especially those modified by man. As outlined earlier in this paper perhaps 50 to 75% of the individuals in the forests across India at latitudes between Bombay and Delhi are migrants from the Palearctic. The lusher forests of south India contain relatively fewer but still large numbers of migrants (Karr, pers. obs.).

According to Medway (1972) 161 bird species are migrants to Malaysia during the northern winter, and most are found in "open or largely deforested country," including aquatic habitats. Ward (1969) also suggests that migrants avoid forest in favor of deforested areas. However, my own data and those of Wells (Table 3) and McClure (Fig. 2) indicate that perhaps 6–15% of the birds in Malaysian forest are Palearctic migrants. Only 24 of the 161 migrants to Malaysia occur in undisturbed forest, and their "importance in the ecology of this habitat is unknown" (Medway 1972). In a survey of Gunong Benom, Medway (1972) found only 11 migratory species in a transect from 200 to 2100 m. Fifteen of 173 (9%) species observed at the Gombak Valley forest in Malaysia and 25 of 145 (17%) species observed at the Khao Yai National Park were migrants (McClure, pers. comm.).

A lowland forest site in Malaysia studied for only 5 days by Medway and Wells (1971) contained 141 species in an area of 200 ha. Adding the observations of several others they accumulated a list of 156 species known from their Kuala Lompat study area. Twelve of these species were migrants and 8 more were partial migrants, species in which "at least some individuals leave Malaysia to breed further north." All species were classified according to habitat. Of the 12 Palearctic migrants, 8 were classed as forest or forest-edge species, 2 as aerial insectivores and 2 were found along rivers or in river bank vegetation. The 8 partial migrants included 6 forest and forest-edge species and 1 each from river edge and aerial sweep species.

In summary, lowland forest habitats seem to be avoided by migrant birds in Africa, and to a much lesser extent in the neotropics. Wintering migrants are more abundant in the lowland forests of India and Malaysia. Forests in India and southeast Asia with high rainfall often have relatively high densities of wintering migrants. Mahabaleshwar for example receives over 6200 mm of rain per year as compared with the 2600 mm for the Panama forest study area. However, over 95% of the rain at Mahabaleshwar falls in the 4-month period—June to September. Nine months of the rainy season are required to accumulate over 95% of the rainfall at the Pipeline Road in Panama. Perhaps

the long dry season in the Indian area has resulted in a low diversity fauna which can easily be invaded by Palearctic migrants. Grassland and open savanna habitats are generally avoided in the neotropics but used very heavily in Africa. The habitats in the lowlands of Africa that harbor greatest densities of migrants are the various forms of semi-arid and dry woodland, while dry forest and second growth and river edge forest in wet areas are used by most migrants that overwinter in the neotropical lowlands. The nearest equivalent to the African semi-arid habitats in Panama is the Cocle Plains areas west of Panama City. Very few migrants occur in that area as winter visitors (Karr, pers. obs.).

Elevation.—For mainland Central and South America there is general agreement that montane and highland (1000 to 2500 m) provide winter homes for more migrants than do similar lowland habitats (Miller 1963, Willis 1966, Leck 1972a, pers. obs.). The Jamaican studies of Lack and Lack (1972) included surveys of mid-level and montane areas of both natural and disturbed habitat. Natural forest above 1000 m elevation contained about the same number of individuals (birds observed per 10 hours) as lowland forest (1.67 vs. 1.49). However, since we will see that migrant densities in the lowland forests are high, we cannot conclude that the high elevation forests of Jamaica have low densities of migrants; rather both lowland and highland areas have high migrant densities. Censuses in mid-level garden and parkland habitats have even higher encounter rates (14.5). No good data on the migrant portion of the fauna are available for mainland Latin America to my knowledge. Miller (1963) suggests that migrants made up about 10 to 15% of the winter avifauna in his cloud forest area at 2000 m elevation in Colombia. This seems a reasonable estimate in my experience. It is similar to the results of Tramer (1974) in dry forest in northern Central America where 6 to 18% of the wintering individuals were migrants. Smith (1975) estimated migrant densities at 1600 m in western Panama at 150 per ha, or 6000 per 40 ha. This seems high to me and may not reflect a general pattern as much as a peculiar local circumstance.

Lowland wet forest data in Panama indicate that winter visitors make up about 1 to 3% of the avifauna. The densities of warblers are much higher in the mid-level forests of Jamaica than in lowland forests but their percentage of the passerine fauna is about the same in the 2 areas, near 30% (Lack and Lack 1972). Despite the high parulid densities, however, there are very few or no birds of groups such as orioles, grosbeaks, thrushes, tyrant-flycatchers, or vireos (Lack and Lack 1972, Ridgely, pers. comm.).

There are conflicting reports on the importance of highland areas as wintering areas for migrants in Africa. Brosset (1968) suggests that highland forests are of some significance in hosting Palearctic migrants but Elgood

et al. (1966) state that the number of wintering species in highland areas is only slightly above the number wintering in wet forest areas. In the forests of Mt. Elgon in Kenya migrants are 10–12% of wintering passerines (Britton 1974). In agreement with Elgood et al., Moreau (1972) says that montane areas in Africa "harbour only a minute proportion of migrants and no species exclusively." That "elevation does not affect the distribution of migrants per se" in Africa (Moreau 1972) is not true in the neotropics. This general pattern is probably related to the extensive savanna and few montane habitats in Africa while in the neotropics the reverse is true.

In southeast Asia, B. King (pers. comm. *in* Leck 1972a) felt that migrants were especially abundant in the mountains of Thailand. My limited observations in the Malaysian highlands (Fraser's Hill) did not yield densities as high as those in neotropical forest at the same elevation, and at the same time of year. Of the 11 migrant species observed by Medway (1972) on Gunong Benom all were restricted to elevations below 1000 m and only 2 were observed above 700 m although some were taken as passage migrants at higher elevations. McClure (1964) reported high migrant densities in the highlands of Malaysia, especially in November and December. Migrants are more abundant in the highlands of Malaysia during southward migration and more abundant in the lowlands during the northward migration (Fig. 2).

Food resources.—Some of the best studies on the impact of migrants deal with patterns of food exploitation. In general, migrants in the tropics harvest superabundant and/or sporadically available resources. These include fruit and nectar (Leck 1971; 1972a,b,c), army ant swarms (Willis 1966), and grass fire and termite-emergence situations (Thiollay 1970b, Moreau 1972). Migrants are usually subordinate to resident species and they generally feed at peripheral or poorer foraging sites whenever residents are present. For example, Willis (1966) points out that migrants are frequently found at the less desirable swarms of *Labidus praedator* rather than swarms of *Eciton burchelli*. In general, it has been concluded that migrants exploit food resources not fully harvested by resident species (Morel and Bourliere 1962, Willis 1966, Thiollay 1970a,b, Moreau 1972). However, Miller (1963) felt that migrants might displace residents in Colombia, forcing them to feed in less competitive situations and even to the extent of restricting their reproductive season. Evidence accumulated to date seems to refute Miller's suggestions. In Sarawak, for example, Fogden (1972) found that the first 3 months of breeding in resident birds coincides with the time when visiting migrants are laying down migratory fat.

Lack and Lack (1972) examined the patterns of resource subdivision among Jamaican warblers (2 residents, 18 migrants) and found marked ecological differences segregating the 20 species. In addition they felt that the warblers

did not significantly share ecological niches with other Jamaican birds. With respect to food types taken, Lack and Lack (1972) found that most species obtain at least 90% of their food as insects. The Cape May Warbler (*Dendroica tigrina*) is the only species that takes major amounts of fruit and nectar in its diet. Ridgely (pers. comm.) found the Tennessee Warbler (*Vermivora peregrina*) feeding on fruits and nectar in Panama. One hallmark of success of a number of migrants in Panama is their ability to switch food resources opportunistically; that is, to exploit available resources as they become available.

Leck (1972a) found that 10% of the feeding visits to fruit trees in Panama lowlands were by migrants compared to 45% in the highlands. In Puerto Rico 60% of the feeding visits to fruit trees were by migrants (Leck 1972c).

Of 34 migrants in Barro Colorado Island forests, 24 (76%) feed on small and 6 (18%) on large arthropods, 3 on small fruit, and 1 species feeds on reptiles and amphibians (Willis, pers. comm.).

Elgood et al. (1966) thought that virtually all terrestrial migrants from the Palearctic to Africa were insectivorous. More recent evidence indicates that perhaps 5% of the migrant species are primarily or exclusively seed eaters (Moreau 1972). However, most of these species winter north of $12°N$, and are therefore out of the area considered here. Blondel (1969), Morel (1968) and others have shown that a number of migrant species exploit fruit resources rather heavily. Warblers of the genus *Sylvia* are known to exploit such fruits as *Lantana cantana* (Moreau 1972, Britton 1974). In my experience in Africa, concentrations of frugivorous species (migrants or residents) typical of the neotropics are rare (Karr 1975).

The competitive interactions of migrants in Africa have been examined from 2 perspectives. Of 90 migrant species in 6 African habitats 14 were without related native species as potential competitors (Moreau 1972). Nineteen others are segregated from native birds by feeding station and 32 differ significantly in size, an indication that they exploit different resources (Moreau 1972). Lack (1971) asked how much competition occurs among congeneric migrants in Africa and found that 64% had no contact with each other due to non-overlapping ranges. Habitat segregated 23%, foraging ecology separated 2%, and no obvious pattern of segregation was discovered for 10% of the species.

I have not been able to find discussions of food resources exploited by Palearctic migrants in Indomalaysia. Insects seemed to me to be the dominant source of food, although fruits are likely taken by some species.

Island vs. mainland.—Previous discussions have already hinted at the differences in migrant abundances and distributions between mainland and island areas. MacArthur et al. (1972) found wintering migrants to be about

25% of the fauna on Puercos Island in the Bay of Panama. This frequency is slightly higher than in the Pipeline Road forest area (Table 2) during the peak of the fall migration, and about 10 times higher than the overwintering (December) density in that forest. Similarly, Terborgh and Faaborg (1973) found island densities in Puerto Rico and Mona Island to be about 10% of the total avifauna. Abundances of migrants on Jamaica were as high as 30% of the total passerine fauna (Lack and Lack 1972).

Leck (1972c) found that the proportion of a fauna composed of migrant species increased from the mainland to islands and as island size decreased. This change was a result of the rapid decline in number of resident species, while the numbers of migrant species remained relatively constant.

Site faithfulness on wintering grounds.—Winter territoriality and long term residence is well documented for migrants on wintering areas. Examples from the neotropics can be found in Schwartz (1964), Willis (1966), Loftin and Child (1967 and papers cited therein), Karr (1971b) and Leck (1972a). Similar results have been reported for Africa (Moreau 1972, Table 19) and Malaysia (Medway 1972). However, as noted above, a number of species are known to change habitats as food availabilities change. Conservation efforts centered on the wintering grounds of migrants must exercise caution in formulating policies.

Conservation efforts in tropical wintering areas.—In a symposium on the avifauna of northern Latin America (Buechner and Buechner 1970) several contributors commented that wintering migrants in Central America are not in danger due to the destruction of forest since most use second-growth habitats as wintering grounds. This may be true for a majority of species but some, such as the Kentucky Warbler, may be specially adapted to wintering at low densities in tropical forest. Such species may be significantly affected by the recent rapid loss of lowland forest. Furthermore, small cleared areas in a mosaic of forest may be the optimal wintering habitat for many species. Extensive cleared areas do not provide that mosaic and will likely provide wintering grounds for few migrants.

In Africa it appears that habitat destruction by man adversely affects migrants (Moreau 1972). This is true not in the early stages of destruction where much second growth remains but rather in the intensively farmed areas south of Lake Victoria and in Nigeria. In these areas the destruction of virtually all shrub and tree growth has a significant effect, reducing migrant densities to near zero. Since no species winter in lowland wet forest of Africa the cutting of these areas should have little or no effect on Palearctic migrants.

SUMMARY

Variation in the intensity and objectives of studies on species which winter in tropical regions makes the derivation of a comparative synthesis difficult. An examination of my

own data combined with a review of published literature shows that the abundance of migrants from the temperate zone varies with (1) vegetation type, (2) elevation, (3) food type, and (4) season within each of the 3 major geographical areas considered in this paper. In addition, there is variation (5) between continents and adjacent islands and (6) among the continents.

With respect to vegetation type, lowland forest habitats are avoided in Africa, but support some birds in the neotropics and in southeast Asia. Grasslands and savannas are generally avoided in the neotropics but used heavily in Africa. Middle to high elevation areas support large numbers of migrants in the neotropics but relatively few in Africa. In southeast Asia the situation varies seasonally and among areas to a greater extent than in Africa and the neotropics.

In general, migrants harvest superabundant and/or sporadically available food resources. This often involves opportunistic shifting of food and habitat types during a single winter season. Migrant abundances seem generally to be highest during the fall passage period, lowest in the winter, and intermediate during the northward migration of the north temperate spring. Some seasonal movements associated with wet and dry season shifts and varying food abundances have been documented in various parts of the tropics. Finally, densities of migrants on islands tend to be higher than densities on nearby mainland areas.

In general, it appears that the evolutionary strategies of migrant birds are keyed to the exploitation of superabundant and/or sporadically available resources in their tropical wintering areas. These resources are often most easily exploited in disturbed, transitory, or isolated patches of habitat.

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